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Author(s)	Alabia, Irene Dolorfino
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学 位 論 文 題 目

Potential habitat of neon flying squid (*Ommastrephes bartramii*) in western and central North Pacific from spatio-temporal models

(西部・中部北太平洋における時空間モデルによるアカイカの潜在的生息域分布の解明)

1.0 Introduction

Neon flying squid (*Ommastrephes bartramii*) is a large pelagic squid inhabiting subtropical and temperate oceans. It is commercially-harvested in North Pacific, where together with other squids, it accounts for roughly 5% of total landings. It is an important component of pelagic food webs, serving as predator of small pelagic fishes and prey for apex predators. In the North Pacific, *O. bartramii* population is comprised of two seasonal spawning cohorts that exhibit pronounced north-south migration driven by spawning and feeding. Environmental conditions forced by local and remote forcing across different spatio-temporal scales could impact squid habitat structures. Hence, the objectives of this research are to examine and characterize the influences of short-middle and long-term changes in the oceanographic conditions to squid potential habitat in western and central North Pacific, using spatio-temporal models fitted with fishery and environmental data. Understanding of species-habitat interactions and their biophysical drivers is imperative for resource management and marine spatial planning.

This research is comprised of five chapters: (1) Seasonal potential habitat of neon flying squid in western and central North Pacific; (2) Summer squid habitat hotspots in the pelagic waters; (3) Squid summer potential habitat from ensemble models for fishery application; (4) Potential squid habitat in response to high-frequency climate oscillations; and (5) Projected impacts of warming ocean to squid potential habitat. The first three chapters fall under short-middle temporal targets and discussed the seasonal drivers of squid potential habitat, identified regions of pelagic hotspots and roles of surface and subsurface features as well as explored the potential of ensemble models forced with vertical temperature and salinity for operational fishery. Chapters 4 and 5 examined squid potential habitat responses under intra-decadal to centennial climate signals and discussed the potential drivers of projected squid habitat patterns. Finally, a brief summary of major highlights, note on present challenges and future research directions will be presented.

2.0 Materials and Methods

2.1 Seasonal squid potential habitat in western and central North Pacific

Following observed patterns in squid jigging data, the study area was divided into 2 regions (140°-150°E and 30°-50°N from December-February; 150°E-160°W and 30°-50°N from May-July). Monthly-compiled commercial squid jigging dataset and environmental factors including sea surface temperature (SST), sea surface salinity (SSS), sea surface height (SSH), eddy kinetic energy (EKE) and wind stress curl (WSC), were used to construct MaxEnt models. Final monthly base models (2001) were validated using jigging points from January-February (winter) and June-July (summer) 2002-2004. Model performance was assessed using threshold-independent metric, area under the receiver operating characteristic (ROC) curve (AUC).

2.2 Squid habitat hotspots in pelagic waters of western and central North Pacific

To examine squid's pelagic habitat hotspots in summer (May-July), a generalized additive model (GAM) that incorporates squid catch per unit effort (CPUE) and five environmental data (SST, SSS, SSH, EKE and mixed layer depth (MLD)) compiled at five-day bin was developed. Monthly model predictions from May-July 2000-2004 were normalized and classified into 0 and 1 using a derived threshold from minimal predicted area (MPA). Habitat persistence (number of years when a particular pixel is classified as squid habitat) across the 5-year period was computed by summing up the binary HSI grids.

2.3 Squid potential habitat from ensemble models for operational fishery

To generate the potential habitat predictions for operational fishery application, I constructed habitat models using 10 model algorithms available from the BIOMOD2 package (Thuiller et al. 2009) in R (ver. 3.1.1) fitted with daily squid fishing points from June-July 1999-2011 and MOVE-4DVAR reanalysis datasets for the vertical temperature, salinity, sea surface height and sea surface height gradient. Based on the arbitrary threshold for the true skill statistics ($TSS \geq 0.65$), a total of 19 models were used to generate daily ensemble predictions for independent squid jigging points for June-July 2012-2014. The ensemble model algorithms were then evaluated against these independent data and assessed based on different evaluation metrics.

2.4 Squid potential habitat in response to high-frequency climate oscillations

To examine summer potential habitat patterns of neon flying squid in relation to high-frequency, ENSO signals, month-specific GAMs were developed using 13-year monthly-compiled squid CPUE, monthly-averaged environmental parameters (SST, SSS, SSH, EKE and MLD) and southern oscillation index (SOI). The isopleths of environmental layers, HSI and anomalies were then analyzed. Monthly HSI anomaly was computed as difference between HSI predictions made from the 13-year median of environmental layers (reference) and monthly HSI predictions from May to July, 1999-2011. Empirical orthogonal function analyses of deseasonalized environmental time-series were used to extract the dominant inter-annual modes of variability and correlate them with SOI (index for El Niño Southern Oscillation: ENSO).

2.5 Projected impacts of ocean warming to squid potential habitat

To investigate the influence of ocean warming to squid summer potential habitat, I used an 11-year (2000-2010, representing present day habitat) jigging data and ten environmental layers to construct preliminary MaxEnt model. Based on the results of variable contribution from AUCs, four variables were then selected for final MaxEnt model. Present-day HSI was generated using median values of environmental factors from 2000-2010 to reduce the effects of outliers to monthly predicted HSI. Finally, to examine the responses of present-day squid potential habitat to projected increase in ocean temperature due to global warming, I used SST projections from four CMIP5 climate models in place of the 11-year median of AVHRR-OI SST while keeping the other three parameters (SSS, SSH and NPP) unchanged, to project squid potential habitat for May to July 2025, 2050 and 2100. Habitat patterns across climate models and years were then compared.

3.0 Results and Discussion

3.1 Seasonal squid potential habitat in western and central North Pacific

The results revealed the seasonal squid potential habitat across different areas of the basin in winter (January-February) and summer (June-July). Distinct regions of squid habitat across different seasons could account for the differences in the relative model contribution of environmental factors. For instance, the high habitat suitability index (HSI) in the eastern coast of Japan in winter could result from favorable forage opportunities enhanced by spin-off eddies off Kuroshio frontal boundary. Southward shift in squid potential habitat from January-February could also be driven by the timing of squid migration to the spawning grounds. In summer, high HSI were found along subarctic frontal zone between 40-45°N, characterized by sharp environmental gradients that could concentrate prey and provide rich forage grounds for squids. The formation of seasonal potential habitat could also reflect the north-south migration of the different squid cohorts.

3.2 Squid habitat hotspots in pelagic waters of western and central North Pacific

The development of habitat hotspots was in sync with the seasonal evolution of favorable forage conditions from early to latter phases of summer. In summer, the critical balance between the light and nutrient gradients enhances primary production, providing rich food source to low- and mid-trophic marine organisms. In May, the habitat hotspots were located in Kuroshio-Oyashio transition zone (TZ) (36-40°N) and gradually shifted north towards SAFZ from June-July. The persistence of squid habitat hotspots across the 5-year period (2000-2004) was highest off SAFZ and lowest across TZ. The dynamics and predictability of oceanographic features could possibly explain for observed differences in persistence of squid hotspots. Hotspots adjacent to predictable and major frontal zone such as SAFZ (33.8) and transition zone chlorophyll-a front (TZCF; 18°C) have higher persistence than those within TZ. Potential habitat hotspots in TZ could be associated with dynamic, short-lived open ocean fronts and eddies, thus, resulting to low hotspots persistence.

3.3 Squid potential habitat from ensemble models for operational fishery

Based on evaluation metric scores derived from ensemble predictions, weighted mean algorithm exhibited highest performance (AUC, TSS and POD). Selected daily HSI maps for June-July 2012-2014 created using weighted mean also showed modest spatial correspondence between predicted HSI and actual jigging sites. Based on HSI patterns derived from ensemble predictions, consistent trend of northward movement of potential squid habitat was also observed and could be in sync with forage-based migration of squid during summer.

3.4 Squid potential habitat in response to high-frequency climate oscillations

The annually-averaged squid potential habitat revealed inter-annual differences in extent and magnitude of high HSI band along the SAFZ in summer. The periods when jigging operations were closest to high HSI band were also characterized by higher observed CPUE. Highest HSI patches were located along 40°N (northern boundary of TZ) branching north towards colder subarctic region (40-45°N; SAFZ). Inter-annual contraction and expansion of high HSI regions were also observed and presumably driven by ENSO-forced environmental variability. Areal-averaged HSI and HSI anomalies along 160E-160W and across 35-45°N from 1999-2011 revealed prominent drop in HSI during strong La Niña (1999 and 2010-2011). During strong El Niño (2009) however, showed a significant HSI enhancement between 42-45°N.

3.5 Projected impacts of ocean warming to squid potential habitat

Projected spatial HSI distributions showed contraction and expansion patterns of squid potential habitats relative to the present-day HSI in western and central North Pacific. From the four CMIP5 AOGCMs, ocean warming events have been detected (with warming intensity proportional to the radiative forcing and CO₂ emissions) and exhibited basin-wide warming patterns. Regional warming differences could account for spatial changes in future HSI projections. Moreover, future HSI maps revealed a northward HSI displacement in response to warm and stratified ocean conditions that might limit sub-surface nutrient transport and consequently, food availability.

4.0 Conclusions, key issues and future directions

Based on the results of this work, important conclusions could be drawn out: (1) the seasonal squid potential habitat is driven by changes in environmental conditions across different regions of the basin (zonal and meridional directions); (2) the squid pelagic hotspots could be driven by the dynamics and predictability oceanographic features; (3) squid potential habitat in pelagic waters responded to the climate-driven (e.g. ENSO and ocean warming) environmental changes. These knowledge could be critical for management of squid fishery resources.

In this thesis, I have also highlighted some of key issues on the (1) availability of data and targeted analyses to elucidate species-environment interaction and (2) future improvements in model prediction accuracy and uncertainty. Future research should be directed towards ecologically-based understanding (e.g. multi-trophic interaction) of squids in pelagic ecosystem.